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Dispositional Properties in Evo-Devo

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Abstract

In identifying intrinsic molecular chance and extrinsic adaptive pressures as the only causally relevant factors in the process of evolution, the theoretical perspective of the Modern Synthesis had a major impact on the perceived tenability of an ontology of dispositional properties. However, since the late 1970s, an increasing number of evolutionary biologists have challenged the descriptive and explanatory adequacy of this "chance alone, extrinsic only" understanding of evolutionary change. Because morphological studies of homology, convergence, and teratology have revealed a space of possible forms and phylogenetic trajectories that is considerably more restricted than expected, evo-devo has focused on the causal contribution of intrinsic developmental processes to the course of evolution. Evo-devo's investigation into the developmental structure of the modality of morphology – including both the possibility and impossibility of organismal form – has led to the utilisation of a number of dispositional concepts that emphasise the tendency of the evolutionary process to change along certain routes. In this sense, and in contrast to the perspective of the Modern Synthesis, evo-devo can be described as a "science of dispositions." This chapter discusses the recent philosophical literature on dispositional properties in evo-devo, exploring debates about both the metaphysical and epistemological aspects of the central dispositional concepts utilised in contemporary evo-devo (e.g., variability, modularity, robustness, plasticity, and evolvability) and addressing the epistemological question of how dispositional properties challenge existing explanatory models in evolutionary biology.

Keywords

developmental constraints; dispositions; evo-devo; evolvability; modularity; robustness; teleology; variational structuralism.

Introduction: Evo-Devo as a Science of Dispositions

One dominant tradition in the history of metaphysics views the denizens of our universe as fundamentally passive: like so many billiard balls, the activity of each ultimately amounts to the degree to which they are "pushed and pulled" by some other. This is in some ways enshrined in contemporary scientific paradigms: what an entity can or must do is conceived as functionally derivative, either due to the contingencies of its extrinsic causal context or as a necessary consequence of the 'laws of nature' which govern it. Another tradition views these modalities as intrinsically grounded in those entities. According to this perspective, the entities which populate our world play an active role in erecting the causal structure. This activity shapes the course of events in virtue of entities possessing properties that specify their potential for (or dispose them to) change.

The former tradition is manifested today by those who defend the idea that the only genuine properties are 'categorical properties.' Categorical properties place no causal or modal constraints on the world. If the world is merely a collection of categorical properties, those constraints are contingent and extrinsic, imbued upon it from a set of higher-order natural laws (which may have been different), or reducible to abstracted reflections of brute facts about its regularities (which may not have occurred). A world constructed from dispositional properties is radically different. Dispositional properties are intrinsically dynamic, essentially defined or individuated by what they do. Their dynamic nature consists in being causally responsible for reliably and repeatedly bringing about a particular type of state of affairs (a

'manifestation') upon the obtaining of a particular set of conditions (a 'stimulus'). Because they are individuated by their functional role in bringing about specific end-states, one and the same dispositional property can be possessed by any number of compositionally or structurally distinct systems (i.e. they are 'multiply realisable'). Furthermore, as the causal roles intrinsic to these properties consist in the potential for the specified production of particular states, dispositions are often understood as teleological, causally directed toward or for those end-states. The intrinsically directed natures of these properties deliver and delimit the space of possibilities for the entities that possess them, and thereby underwrite patterns of causal regularities we observe.

Although contemporary metaphysics is currently experiencing a neo-Aristotelian revival of sorts, especially within the philosophy of science, dispositional ontologies have historically been viewed with suspicion in theoretical biology. From the perspective of the long-standing paradigm of the Modern Synthesis, there are several reasons why this might be the case. The most obvious stems from a general distrust of teleological analyses of natural phenomena: it considered the commitment to a thoroughly mechanistic, non-purposive view of nature, as ushered in by the Scientific Revolution, as incompatible with assigning any explanatory role to the goal-directedness of organisms (Grene and Depew 2004). This demanded a rejection of teleological analyses such as the theory of orthogenesis – the view that the evolutionary history of organisms was guided by an intrinsic impetus oriented toward some predefined goal (Mayr 1992). It is often claimed that Darwin's non-teleological explanation of adaptation effectively dissolved this problematic perspective. However, according to Mayr, the viability of a teleological characterisation of life only vanished with the advent of the Modern Synthesis in which biological disciplines collectively rejected the existence of all (phenomenal or causal) finalism. With palaeontology proving the absence of privileged evolutionary trends and molecular biology demonstrating the intrinsic randomness of the process of genetic change, the study of evolution by natural selection became reduced to the statistical analysis of changes in population gene frequencies (Walsh 2015).

In identifying intrinsic molecular chance and extrinsic adaptive pressures as the only causally relevant factors in the process of evolution, the Modern Synthesis perspective strongly suggested that an ontology of dispositional properties in biology was untenable. On one hand, its dependence upon the absolute randomness of variation effectively disavowed the study of 'the possible' as a legitimate epistemological goal of evolutionary theory. Because every and any form can theoretically arise from random mutations, the proper study of evolution *via* population genetics had to be focused solely on actual variations. On the other hand, its insistence that the evolutionary trajectories of populations were explicable only as the result of the process of natural selection effectively relegated the explanatory power of intrinsic factors to a position of theoretical irrelevancy. From the outlook of the Modern Synthesis, if the central *explanandum* was adaptive change, then functionally designated developmental processes were passive, being "pushed and pulled" by the selective forces of their environments. As a result, evolutionary biology was framed as a science of the external.

However, since the late 1970s, an increasing number of evolutionary biologists have challenged the descriptive and explanatory adequacy of this "chance alone, extrinsic only" understanding of the process of evolution. Recent morphological studies of homology, convergence, and teratology have revealed that the space of possible forms and phylogenetic trajectories is considerably more restricted than expected. Evo-devo, in contrast to the approaches of evolutionary biology founded in the Modern Synthesis, focuses on the causal contribution of intrinsic developmental processes in shaping that space, and with it the course of evolution. Evo-devo's investigation into the developmental structure of the modality of morphology – the possibility and impossibility of organismal form, as well as the directionality and speed of morphological changes – has led to the utilisation of dispositional concepts that emphasise the 'inherency' of the evolutionary process, its proclivity to privilege particular pathways (see the chapter on

"Inherency"). In this sense, and in contrast to the perspective of the Modern Synthesis, evo-devo can be described as a "science of dispositions" (Austin 2017).

This chapter discusses recent philosophical literature on dispositional properties in evo-devo. The first section explores debates about the metaphysical and epistemological aspects of the central dispositional concepts utilised in evo-devo: developmental constraints and variability, modularity, robustness, plasticity, and evolvability. The second section addresses the epistemological question of how dispositional properties challenge existing explanatory models in evolutionary biology.

Dispositional Concepts in Evo-Devo

From constraints to variational properties

The differences between the explanatory agendas of standard evolutionary biology and evo-devo might be seen as a translation of the relationship between actual and possible. In the 1980s, with the rise of molecular biology and the explanatory project of adaptationism, the concept of 'developmental constraints' was understood "negatively" as the observable limits of molecular variation and selective optimisation within populations (Brigandt 2015b). In contrast to the insistence on the ability of natural selection to explain the shape of any morphological form as one causally carved from extrinsic, adaptive forces, morphologists and developmental biologists became increasingly interested in the apparent intrinsic "resistance to change" that certain morphologies, such as homologues and body plans, seemed to exhibit over evolutionary timescales, and the corresponding "forbidden" areas of morphospace that remained unoccupied in existing phylogenies (see the chapter on "Developmental Constraints").

In recent years however, evo-devo biologists have highlighted the generative power of constraints. On this understanding, the causal architectures of developmental systems not only constrain the set of possible forms, but also actively provide new opportunities for evolutionary change (Brigandt 2015b). The role of development in the process of evolution is not simply to constrain, but to determine what is morphologically possible, and among these possibilities, what is more likely. On this "positive" conception of constraints, developmental systems facilitate morphological change and thus are capable of playing a central role in the explanation of macroevolutionary transformation and evolutionary novelty. In contemporary evo-devo, concepts like 'variability' (as opposed to 'variation') capture this positive role of constraints as generative capacities: while variations are "the actually realised differences between individuals", "variability is a term that describes the potential or the propensity to vary" (Wagner and Altenberg 1996). Indeed, some authors have advocated abandoning the notion of developmental constraints altogether in favour of conceptualising developmental systems as possessing "variational properties": diverse generative capacities causally responsible for the production of a wide range of phenotypes (see the chapter on "Mechanisms of Pattern Formation, Morphogenesis, and Evolution").

While the concept of developmental constraint situates the conflict between populational and developmental approaches to evolutionary change in the context of the dichotomy between externalism and internalism, utilising the concept of variability allows one to emphasise the differences between the epistemological aims of population genetics and evo-devo, thereby making clear their distinct theoretical commitments – the former to the 'actual', the latter to the 'possible' (Eble 2003). Evo-devo biologists explicitly recognise the tension between these two perspectives, noting that while variation "can be directly observed as a property of a collection of items", variability "belongs to the group of 'dispositional' concepts", as the "variability of a phenotypic trait describes the way it changes in response to environmental and genetic influences" (Wagner and Altenberg 1996, p. 969). For this reason, Gunter Wagner coined the term 'variational structuralism' to denote the ontological commitments of evo-devo in contrast to those of the Modern Synthesis according to which "all that is real are the realised differences

among organisms, and not their underlying variational tendencies" (Wagner 2014, p.19; see also the chapter on "Typology and Natural Kinds in evo-devo").

Modularity

The development of an organism's morphological features does not happen all at once, or even all together; it is a process of compartmentalised collaboration. Each 'developmental module' that participates in that process is characterised by a high degree of internal causal connectivity among its constituents, a prominent form of which consists in the tightly-knit regulatory domains of a genetic regulatory network's transcription factors, cis-regulatory sites, and signalling cascades (see the chapter on "Modularity"). Because these semi-autonomous organismal sub-systems govern the generative specificities of morphological development and have their own traceable intra- and inter-species phylogenetic histories, they are of prime importance in evo-devo research.

From a developmental perspective, these sub-systems appear to operate dispositionally, as centres of specified morphological potentiality. They causally mediate the influence of chemical stimuli—from cellular signaling to downstream genetic expression pattern—to reliably and regularly initiate the production of particular morphological features. These modules exhibit a high degree of robustness such that mutational variations among their component elements and epigenetic variations in their regulatory structure generally have little to no effect on their generative competence to produce morphological structure (see the chapter on "Robustness"). Over time then, and in successive generations, the generative role played by a particular complex of genetic elements in a specific regulatory configuration can become 'autonomised', gaining a kind of independence from its original underlying genetic architecture. This autonomy is manifested via multiple realisation by a number of distinct generative structures over developmental, and eventually evolutionary time-scales (see the chapters on "Developmental Homology" and "Developmental System Drift").

Because of this autonomy, the storied pasts of these modules can only be deciphered with some difficulty, and it is conceptually advantageous to individuate them functionally, according to the specific causal role they perform in the production of organismal morphology. Given the molecular heterogeneity of a single module's multiple genetic underpinnings over time, that generative role is quite complex: it encompasses not only the production of one or a few morphological configurations, but an entire 'morphospace' of quantitative and qualitative variations of them (see the chapter on "Morphological disparity"). Importantly, however, the generative potential which is mapped-out in these morphospaces are reflections of the intrinsic capacities of these modules, capacities which channel the exploration of these spaces over evolutionary time (see the chapter on "Inherency"). As multiply realised, intrinsic centres of specified potentiality that both conform and constrain the character of morphological regularities in the phylogenetic record, developmental modules are best conceptualised dispositionally (Austin 2017).

One of the major goals of evo-devo is unravelling the developmental basis of variational modularity, or the variational independence among characters. In this context, modularity is understood as a property of the whole genotype-phenotype map which determines how variation is structured (see the chapter on the "Genotype-Phenotype Map"). Therefore, variational modularity is not a disposition to generate particular morphological features, but a disposition to generate variation in a particular way. The modularity of the genotype-phenotype map seems crucial for the ability of developmental systems to evolve, insofar as the organisation of development into semi-autonomous processes leads to the independent variation of characters which can function as "building blocks" of phenotypic adaptation (see the section on Evolvability).

Furthermore, although this developmental and evolutionary autonomy of modules is secured by the high degree of causal integration among their constituents, they are at the same time typified by their tolerance to alterations in this dynamic architecture. Modular systems thus possess the capacity to preserve their generative competency throughout modifications to their causal-temporal structure, an ability secured by a number of complex network features (see the section on Robustness). This dispositional aspect of modular systems is of major evolutionary significance as it is correlated with the phenomenon of developmental plasticity: the ability of a single module to produce an array of differing phenotypes crucially depends upon this capacity for compositional flexibility (Walsh 2015; see also the section on Plasticity). Moreover, this capacity is itself subject to evolutionary modification, as illustrated in recent studies on the developmental basis for variational independence among particular traits in particular species (see references in Wagner *et al.* 2007). For instance, forelimbs and hindlimbs appear to be ancestrally correlated, but in bats this correlation is broken – a separation which subsequently facilitated the specialisation of the forelimb for flying. Thus, understanding how interconnections within and among modules originate, break down, and change throughout evolutionary time is a major research agenda for evo-devo (Bolker 2000).

Robustness

In developmental biology, robustness (also referred to as canalization or developmental stability) refers to the ability of developmental trajectories to buffer against environmental or genetic perturbations that would otherwise affect a phenotypic outcome (see the chapters on "Robustness" and "Canalisation"). Robust systems are both persistent – able to maintain the causal production of an end-state by means of compensatory changes within the system – and pleonastic – able to bring about that end-state via a number of alternative pathways. Because these homeostatic phenomena represent a system's causal bias toward some particular state, they are standard marks for those systems being 'goal-directed' (Walsh 2015; see also the chapter on "Teleology").

The pleonastic robustness of biological systems is exhibited in their privileging of a limited set of developmental trajectories. As illustrated in Waddington's epigenetic landscapes, and more recently in biological models developed from dynamic systems theory, these systems promote morphological invariance because their constitutive causal architecture is dynamically oriented toward the production of a limited set of developmental fates from a wide variety of initial (and intermediate) states (Brigandt 2015a). In grounding the intrinsic developmental stability of a system by dynamically privileging the production of a particular morphology, and thus the regularity of the system's operation in pursuit of that end within a wide range of environmental and developmental contexts, pleonastic robustness is a system-level exhibition of dispositionality.

The homeostatic behaviour exhibited in persistence-based robustness is typically secured in one of two ways. First, biological systems can be constituted by a regulatory network that possesses a number of 'redundant' elements, which can take-up the causal slack of missing, mutated, or disabled elements. Second, these systems exhibit a 'degenerative' capacity to "re-wire" their regulatory architecture, producing new causal connections in novel configurations to maintain their function under significant perturbation. Importantly, in these more extreme exhibitions of homeostatic phenomena, the system maintains a generative proclivity toward a specific morphological end-state that persists throughout the alteration of its compositional elements and their causal architecture. This multiply realised, goal-directed capacity to produce and dynamically preserve the production of an end-state occupies a principal position in the explanatory framework of evo-devo, providing an important link between ontogeny and phylogeny.

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The project of analysing and understanding developmental systems' propensity for invariance is central to evo-devo: not only does this feature of systems illustrate one of its central tenets – that the modality of organismal morphology has an intrinsic, developmental basis – but it also serves as an important theoretical tool with which it conceptualises the stability (and thus, selectability) of phenotypic traits over evolutionary time-scales. On the one hand, these systems' generative stability throughout a variety of structural perturbations undergirds the ability of organisms to maintain their morphological integrity within various environmental conditions – a capacity which is positively correlated with their potential for selective success. On the other hand, the generative stability of these systems throughout mutational variations at the same time allows for their accumulation of developmental resources which, while not immediately divertive of their generative function, may eventually contribute to the production of morphological novelties when the system undergoes further genetic or environmental alterations – this amassing of 'cryptic variation' thus enhances the evolvability of these systems (see the chapters on "Canalisation", "Developmental Systems Drift", and "Epigenetic Innovation").

Plasticity

The ability of organisms to produce distinct phenotypes in distinct environments is an extremely pervasive phenomenon, one evidenced in everything from simple seasonal-based changes in colouration to the complex predator-based alterations of defensive morphologies. In developmental biology, phenotypic plasticity is invariably described in dispositional terms as the ability of an organism to alter its phenotype in response to changes in its environment, or as the potential of a genotype to produce a number of alternative phenotypes in the context of distinct environmental conditions (see the chapter on "Developmental Plasticity and Evolution"). While in a certain sense the plasticity of developmental systems can be understood as an inverse measure of their generative robustness, the two phenomena are in another sense both exemplifications of those systems' ability to develop a functional phenotype (Brigandt 2015a). In this latter sense, both are exhibitions of persistent and pleonastic processes, and together serve as "the very paradigm of goal-directed activity" (Walsh 2015).

The phenomenon of phenotypic plasticity demonstrates that the goal-directedness, or causal privileging of developmental systems toward the production of a particular phenotype is not a unidimensional affair: alterations in the environmental conditions and thus, heterochronical and heterotopical alterations in the upstream signalling of these systems (that is, changes in their 'stimulus' conditions) can result in downstream qualitative alterations – in shape, size, pigmentation, etc. - of its phenotypic product (that is, its 'manifestation'). The goal-directed capacities of developmental systems are thus 'multi-track' dispositions, able to produce a range of quantitatively and qualitatively distinct manifestations in response to a variety of distinct stimulus conditions (Vetter 2013). The set of potential manifestations of a developmental system's multi-track disposition may form a continuous, gradient-like stratification of phenotypic variation – as exemplified in the 'reaction norms' of experimental genetics – or consist of a collection of discrete phenotypic forms (so-called 'polyphenisms'). Thus the developmental dispositions of these systems cannot be individuated according to their generative competency with respect to the production of a single, particularised phenotypic end-state, but rather to their potential to produce an entire "phenotypic repertoire" (Austin 2017).

Developmental plasticity has been shown to have a major role in adaptive evolution, and has even led to the foundation of a new discipline, ecological developmental biology (or eco-evo-devo) that incorporates the central role of the environment in our understanding of developmental evolution (see the chapter on "Eco-evo-devo"). While evolution is typically regarded as a process through which organisms passively generate random variation and become better adapted to the external demands of their environment, developmental plasticity integrates the constitutive role of the environment in the very generation of

variation. Like robustness, plasticity is an adaptive response to external conditions. However, plastic responses to environmental changes can also lead selection, preceding and enabling adaptive change. Thus, in "plasticity-first" models of evolution, novel phenotypes are conceptualised as originating by means of environmental changes that only subsequently are genetically stabilised. In this way, the intrinsic capacities of organisms for specified phenotypic variation can be seen as a significant factor in determining the directionality of the process of evolution.

Evolvability

Evolvability, or the capacity of biological systems to evolve, is widely understood as a cornerstone of evo-devo (Hendrikse *et al.* 2007; see also the chapters on "Developmental Evolvability" and "Variational Approaches to Evolvability: Short-and Long-Term Perspectives"). Efforts have been made to precisely define evolvability and philosophers have shown an interest in conceptualising it dispositionally. While some have argued for a unified concept (Sterenly 2007; Brown 2014), biologists by and large understand evolvability as having a multiplicity of referents (Pigliucci 2008; Nuño de la Rosa 2017). Evo-devo research on evolvability concentrates on how the properties of developmental systems, such as modularity, plasticity or robustness, affect the generation of heritable phenotypic variation on which natural selection can act (Wagner and Altenberg 1996; Kirschner and Gerhart 1998). In this sense, the concept of evolvability refers not only to the generation of possible forms, but also to possible adaptations. Thus, whereas developmental constraint and variability are primarily morphological concepts that articulate the causal relationship between genetic and phenotypic variation, the concept of evolvability incorporates a functional dimension to the explanatory framework of developmental evolution, operating as a conceptual tool to understand the relation between variability and adaptation.

Philosophers of biology typically construe evolvability as a probabilistic dispositional property. In contrast to ordinary, deterministic dispositions, which manifest in the presence of appropriate stimulus conditions, a lineage may fail to evolve even when it has the capacity to do so. If we understand evolvability as a population-level property, its probabilistic character is evident: the manifestation of evolvability is a function of various stochastic processes within populations, and therefore natural selection may or may not select the most evolvable (from a developmental perspective) populations (Love 2003; Sterenly 2007; Brown 2014). However, in evo-devo research, the probabilistic character of evolvability can also be understood as an intrinsic consequence of organism-level, genotype-phenotype mappings that determine whether "the probability that random mutation will improve the phenotype has increased during evolution" (Pavlicev and Wagner 2012). The capacity to evolve is generally understood as an intrinsic property of biological systems in evo-devo, which is dependent on their genetic composition and associated developmental architecture. However, philosophers of biology have challenged this assumption arguing that, given their causal influence on mutation rates, environmental (extrinsic) factors, such as geographic range or temperature, must be included in the "causal base" of evolvability, a requirement which plausibly calls into question the intrinsicality of the capacity (Brown 2014; Love 2003).

While the fact that phenotypes vary in their propensities to respond to natural selection is widely accepted, the idea that evolvability itself is the subject of selection, and can therefore evolve remains highly contested. The mainstream position is that the evolution of evolvability would entail an untenable teleological approach to evolution according to which natural selection produced adaptations for future, unknown environments (Sniegowski and Murphy 2006). However, this is not necessarily the case: evolvability may evolve simply as a by-product. For instance, the fitness advantages conferred by developmental modularity may have led to its selection, which would in turn have had long-term consequences for adaptive evolution. In these sorts of cases, natural selection would act on the effects associated with the variational capacities of developmental systems, thus indirectly enhancing evolvability.

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Dispositional Properties and Explanatory Models in Evo-Devo

Evo-devo is defined not only by its adoption of a novel set of conceptual tools, but also by its utilisation of them in constructing explanatory frameworks to understand both development and evolution (see the chapter on "Explanation"). Because its conceptual toolbox is thoroughly dispositional, the explanatory models of evo-devo stand in stark contrast to those of the Modern Synthesis: they appeal to the efficacy of the intrinsic, dynamic capacities of developmental systems to shape the course of evolution. In doing so, these models follow in the spirit of the proposal to re-conceptualise 'fitness' as a propensity, or disposition to survive and reproduce, rather than as a measure of the actual number of offspring of an organism (Mills and Beatty 1979).

One of the most central schemas employed to conceptualise the process of evolution that arose from the ontological commitments of the Modern Synthesis was the distinction between proximate and ultimate causation (see the chapter on "Proximate-Ultimate Causation"). According to Mayr, proximate causes (e.g. developmental and physiological factors) and ultimate causes (e.g. natural selection, selective drift) necessarily address distinct 'how' and 'why' questions. These distinct question types constitute the explanatory agendas of independent biological disciplines: functional biology (how) and evolutionary biology (why). Although Mayr acknowledged that developmental processes have a unique causal role to play in biological explanations (even one involving the goal-directedness of their operation), he nevertheless considered them irrelevant to the explananda of evolutionary biology; answers to the 'how' questions of development are unable in principle to feature in the answers to the 'why' questions of evolution (Mayr 1992). According to this dichotomy, embedded in the theoretical framework of the Modern Synthesis, developmental systems are intrinsically inert with respect to the process of evolution. They are "pushed and pulled" by the extrinsic forces of selection, and hence incapable of playing an important explanatory role with respect to that process.

Philosophers of biology have recognized that Mayr's proximate-ultimate dichotomy is a framework into which the explanatory agenda of evo-devo cannot be situated comfortably. The aim of evo-devo is to integrate the causal influences intrinsic to the process of development into our understanding of evolution. This is a goal that can only be accomplished by adopting a more "reciprocal" model of biological causation wherein the proximate factors operative within those processes, together with natural selection, are understood as proper, active causes of evolutionary change. For example, in offering "lineage explanations" which provide detailed information about the actual sequential changes in developmental mechanisms which have causally undergirded phenotypic changes over time, the explanatory framework of evo-devo necessarily includes aspects of both proximate and ultimate explanations (Calcott 2009; see the chapters on "Explanation", "Evo-Devo and Phylogenetics", and "Proximate-Ultimate Causation"). Furthermore, "ultimate", lineage-based explanations that appeal to actual evolutionary trajectories do not exhaust the kind of evolutionary explanations (indeed, the most characteristic kinds of explanations) employed in evo-devo, precisely because the latter depend upon the dispositional properties of biological systems. Explanations involving 'evolvability' appeal to the intrinsic disposition of a population to evolve, to "differences in the internal (rather than external) features of populations that increase the probability of a particular evolutionary outcome in the future (for example, adaptedness, diversity)" (Brown 2014, p.560). These types of explanations, characteristic of and crucial to evo-devo, are ones in which the intrinsic potentialities of developmental systems shape the contours of an adaptive landscape and possess the relevant explanatory power with respect to the actual characteristics of a particular lineage.

From a developmental perspective, one of the most prominent and successful explanatory programmes employed in evo-devo research consists in the utilisation of mechanistic models (see the chapter on "Mechanisms"). Mechanistic explanations offer predictive utility about some target phenomenon in virtue

of conceptualising it as the causal product of a step-wise, temporally successive series of state-changes in a structurally organised set of discrete elements. While an explanatory schema that appeals to the actual organisation and regular operation of mechanistic components is powerfully predictive in many molecular contexts, "in evo-devo … there are important scientific questions that are not just about the actual behaviour of a mechanism, but also its dispositions" (Brigandt 2015a, p.162). This is because explaining robustness, plasticity, and modularity (inter alia) requires an appeal to the capacities of developmental systems to either react to perturbations or permit modifications. Genuinely explanatory models of these phenomena must not only represent their mechanistic structure, but also their dynamic potentiality for the alteration of that structure. Properly capturing the dynamics of developmental systems, and thus adequately measuring their role in shaping the modal structure of the evolution of morphology, may even require the utilisation of non-mechanistic models like those of 'dynamical systems theory,' which are increasingly prevalent in evo-devo analyses of everything from robustness to evolutionary novelty (see the chapters on "Modeling and Simulation" and "Modelling Evolution of Developmental Gene Regulatory Networks").

Cross-references

Developmental Constraints
Developmental Homology
Developmental Plasticity and Evolution
Evo-Devo as a Discipline
Evo-Devo and Phylogenetics
Developmental Evolvability
Epigenetic Innovation
Explanation
Extended Evolutionary Synthesis
Inherency
Mechanisms
Modelling and Simulation
Modelling Evolution of Developmental Gene Regulatory Networks
Modularity
Proximate-Ultimate Causation
Robustness
Teleology
Typology and Natural Kinds in Evo-Devo
Variational Approaches to Evolvability: Short-and Long-Term Perspectives

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